abrasus and *M. temminckii*. Both showed C-bands in all centromeres. Additionaly *M. abrasus* presented a C-band in the telomeric region of the short arms of the largest acrocentric pair, and *M. temminckii* a C-band in the satellite region of the short arm of a large acrocentric pair. We found in *Molossus molossus* blocks of pericentromeric constitutive heterochromatin in 22 of the 23 autosome pairs and in the X. However, this species presents rather different G-bands from those reported for *M. abrasus* and *M. temminckii*. In addition, nucleolar organizing regions were found in one pair in *M. molossus* while *M. abrasus* presented such regions in five small chromosomes, and *M. temminckii* in three pairs.

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Zusammenfassung

G-, C- und NOR-angefärbte Karyotypen von zwei Fledermausarten aus Südbrasilien (Chiroptera: Vespertilionidae, Molossidae)

Es werden Standardkaryogramme sowie G-, C- und NOR-gefärbte Metaphasen von zwei Fledermausarten aus Südbrasilien beschrieben. Je 7 Männchen und Weibchen von *Eptesicus brasiliensis* (Vespertilionidae) und 3 Männchen und 13 Weibchen von *Molossus molossus* (Molossidae) wurden untersucht. Die cytogenetische Analyse ergab 2n = 50 and AN = 48 für *E. brasiliensis* and 2n = 48 and AN = 54 für *M. molossus*. Bei *E. brasiliensis* sind alle Autosomen akrozentrisch; *M. molossus* weist 4 Paare submetazentrischer und 19 Paare akrozentrischer Chromosomen auf. Beide Arten haben ein akrozentrisches Y-Chromosom, das X-Chromosom ist submetazentrisch bei *E. brasiliensis* and metazentrisch bei *M. molossus*. Die Muster der G-Bänder bei *E. brasiliensis* unterscheiden sich nicht von denen anderer *Eptesicus*-Arten. Dagegen unterscheidet sich *M. molossus* deutlich von anderen Arten der Familie. Bei den C-Bändern ergaben sich keine wesentlichen Unterschiede. Bei beiden Arten ließen sich NORs nur in einem Chromosom anfärben, welches eine sekundäre Einschnürung in der Nähe des Centromers aufweist.

References

Ando, K.; Tagawa, T.; Uchida, T. A. (1977): Consideration of karyotypic evolution within Vespertilionidae. Experientia **33**, 877–879.

Ando, K.; Tagawa, T.; Uchida, T. A. (1980): The C-banding of Japanese species of vespertilionine bats (Mammalia: Chiroptera). Experientia **36**, 653–654.

Baker, R. J.; Lopez, G. (1970): Karyotypic studies of the insular populations of bats on Puerto Rico. Caryologia **23**, 465–472.

Baker, R. J.; Haiduk, M. W.; Robbins, L. W.; Cadena, A.; Koop, B. F. (1982): Chromosomal studies on South American bats and their systematic implications. In: Mammalian Biology in South America. Ed. by M. A. Mares, and H. H. Genoways. Pittsburgh Special Publication Series. Pymatuning Laboratory of Ecology, Univ. Pittsburgh. Vol. **4**, 303–327.

Bickham, J. W. (1979): Chromosomal variation and evolutionary relationships of vespertiolionid bats. J. Mammalogy **60**, 350–363.

Emmons, L. H. (1990): Neotropical rainforest mammals, a field guide. Chicago: Chicago University Press.

Howell, W. M.; Black, D. A. (1980): Controlled silver-staining of nucleolus organizer regions with a protective colloidal developer: a 1-step method. Experientia **36**, 1014–1015.

Koopman, K. F. (1982): Biogeography of bats of South America. In: Mammalian Biology in South America. Ed. by M. A. Mares and H. H. Genoways. Pittsburgh Special Publication Series. Pymatuning Laboratory of Ecology, Univ. Pittsburgh. Vol. **4**, 327–332.

Lee, M. R.; Elder, F. F. B. (1980): Yeast stimulation of bone marrow mitosis for cytogenetic investigation. Cytogenet. Cell Genet. **26**, 36–40.

McBee, K.; Bickham, J. W.; Yenbutra, S.; Nabhitabhata, J.; Schlitter, D. A. (1986): Standard karyology of nine species of vespertilionid bats (Chiroptera: Vespertilionidae) from Thailand. Ann. Carnegie Mus. **47**, 361–383.

McBee, K.; Schlitter, D. A.; Robbins, R. L. (1987): Systematics of African bats of the genus

Eptesicus (Mammalia: Vespertilionidae). 2. Karyotypes of African species and their generic relationships. Ann. Carnegie Mus. **56**, 361–383.

Morales, J. C.; Ballinger, S. W.; Bickham, J. W.; Greenbaum, I. F.; Schlitter, D. A. (1991): Genetic relationships among eight species of *Eptesicus* and *Pipistrellus* (Chiroptera: Vespertilionidae). J. Mammalogy **72**, 286–291.

Morielle-Versute, E.; Varella-Garcia, M.; Taddei, V. A. (1991): Variação cromossômica no gênero *Molossops* (Molossidae, Chiroptera). Rev. Bras. de Genética **14** (3, suppl.), 60.

Patton, J. C.; Baker, R. J. (1987): Chromosomal homology and evolution of phyllostomatoid bats. Rev. Sys. Zool. **27**, 449–462.

Seabright, M. (1971): A rapid banding technique for human chromosomes. Lancet **2**, 971–972.

Silva, F. (1985): Guia para determinação de morcegos: Rio Grande do Sul. Porto Alegre: Martins Livreiro.

Sumner, A. T. (1972): A simple technique for demonstrating centromeric heterochromatin. Exp. Cell Res. **75**, 304–306.

Varella-Garcia, M.; Morielle-Versute, E.; Tadei, V. A. (1989): A survey of cytogenetic data on Brazilian bats. Rev. Bras. Genetica **12**, 761–794.

Volleth, M. (1987): Difference in the location of nucleolus organizer regions in European vespertilionid bats. Cytogenet. Cell Genet. **44**, 186–197.

Warner, J. W.; Patton, J. L.; Gardner, A. L.; Baker, R. J. (1974): Karyotypic analysis of twenty-one species of molossid bats (Molossidae:Chiroptera). Can. J. Genet. Cytol. **16**, 165–176.

Williams, D. F. (1978): Taxonomic and karyologic comments on small brows bats, Genus *Eptesicus*, from South America. Ann. Carnegie Mus. **47**, 361–383.

Zima, J. (1982): Chromosomal homology in the complements of bats of the family Vespertilionidae. II. G-band karyotypes of some *Myotis*, *Eptesicus* and *Pipistrellus* species. Folia Zoologica **31**, 31–36.

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Observations on the postnatal behavioural development in the Marsh mongoose (*Atilax paludinosus*)

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Abstract

Marsh mongooses (*Atilax paludinosus*) are solitary, nocturnal herpestines. This study describes postnatal behaviour patterns in naturally reared and hand-raised animals. First appearance of nine different categories was recorded. Comparisons were made with postnatal behavioural development in other herpestines, in order to assess to what extent it reflects the phylogeny of the subfamily.

Introduction

Postnatal physical development in marsh mongooses is documented (Frese 1980; Baker and Meester 1986), but there is no literature on postnatal behavioural development. Unlike the more sociable Herpestinae, *Atilax* is solitary and shows no co-operative behaviour in raising young. Differences in the development of postnatal behaviour patterns amongst herpestines may be attributed to their divergent rearing systems. In order to investigate this suggestion, this study describes postnatal behaviour patterns of both naturally reared and hand-raised *Atilax*, and compares it with the rate and pattern of development in other herpestines.

Material and methods

The thirteen animals here reported on originated from five captive matings and two wild matings. Naturally reared mongooses were maintained in outdoor enclosures measuring 1.5 × 3 × 1.2 m, while hand-raised animals were reared indoors in a room measuring 2 × 3 m. The milk formula fed to hand-reared animals consisted of one part tinned, evaporated, unsweetened milk (brand name Carnation) to two parts of water. To each 500 mls of constituted milk compound, 5 mls of glucose and 2 mls of multivitamin syrup (brand name Vi-daylin) were added. Mongooses were bottle-fed, using miniature (30 ml capacity) glass bottles with rubber teats, at three- or four-hourly intervals for the first 14 days, and thereafter at four-hourly intervals during daylight hours only, until weaning commenced. During weaning feeds were spaced at five-hourly intervals. First solids offered to the mongooses were finely chopped oxheart and chicken. Naturally reared animals were undisturbed and entirely raised by their mother.

First appearance of behaviour patterns were recorded and descriptions of the patterns were made.

Results

Table 1 provides details of the mongooses described in this study. Concern over the survival of the young in the presence of the father prompted removal of two of the four male mongooses from the females as soon as pregnancy was established (Baker and Meester 1986). As a result these litters (A1 and E2) were exclusively reared by the mother. On three other occasions the males had access to the females during parturition. Firstly

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(litter B1), the male remained in the enclosure for three days after parturition but was excluded from the "nursery nestbox" by the female and played no role in rearing the offspring. Secondly (litter E1), three young were born, one of which was killed and eaten by the mother who was agitated by the presence of a male and female. The remaining two offspring survived as a result of hand-rearing. On the third occasion (litter G1) two young were removed for hand-raising when their littermate was found dead.

Table 1. **Details of the animals from which data were gathered**

Litters	Mating	Offspring		Natural (N)/ Hand-reared (H)
		♂♂	♀♀	
A1	Captive	AA; AB	AC	N
B1	Captive		BA; BB	N
E1	Captive	EB	EA	H
E2	Captive	EC; ED		N
G1	Captive	F	D	H
–	Wild		E	H
–	Wild		K	H

Parturition occurred at night (between 18.30 h and 03.00 h), and in one instance (litter E1) it lasted 4.5 hours. The mother ate little or nothing of the normal food provided on the night of parturition. While activity patterns were normal until the evening of parturition, the female remained comparatively inactive during the birth, and remained within the nestbox. Nesting material was not used and on the completion of the birth the female remained with the young.

Maternal care involved suckling, stimulating excretion, protection and transmitting skills to the young. In the first few weeks the mother prompted elimination by licking the ano-genital region of her young, and then consumed the products. If the mother became agitated or was disturbed when she had a very young litter, she usually picked up a single youngster in a neck-grip or scruff-hold, and ran about the cage as if attempting to escape from the source of 'danger'.

In naturally reared litters, young became mobile outside the nestbox on day 23 at the earliest, but more commonly this happened only by day 28. As soon as exploration began, the mother kept a close watch over the young and, in the event of 'danger', she retrieved them by means of a scruff-hold, transporting them to the safety of the nestbox. As the young matured they became less docile and attempted to re-emerge as soon as the mother had retrieved them. On these occasions she simply blocked the nestbox entrance or held the young by the scruff until the 'danger' had passed. By day 61 the young avoided retrieval by the scruff-hold, and the mother attempted to 'herd' them back to safety. When 'herding' the mother directed the young by moving quickly beside them and nudging them forwards.

Table 2 provides details of the onset of behaviour patterns exhibited by both naturally reared and hand-reared mongooses. Apart from sucking and attention vocalizations (the attention call and grizzling), crawling and inefficient scratching, the alarm response was the earliest behaviour pattern to emerge. The feeding growl coincided with the development of weaning. Play became apparent as locomotory capacities improved, while the development of scent-marking was closely followed by the onset of cackle vocalizations. Sibling fighting and copulatory behaviour were the last behaviour patterns to develop.

While crawling was the first locomotory activity recorded, it was inefficient for the first few days. Young mongooses were scarcely able to lift the belly off the ground, and movement was shaky. Direction was random and only short distances were traversed. The grizzle vocalization accompanied all early forms of locomotion.

Table 2. Average age (in days) of first appearance of postnatal behaviour patterns in *Atilax paludinosus*

Behaviour	Naturally-reared Mean age (days)		Hand-reared Mean age (days)		Significance (p = 0.05)	
Vocalizations						
Attention	–		0–38	n=2		
Grizzle	0	n=7	0	n=6		
Food	34.4	n=7	33.3	n=3	t=0.35	NS
Cackle	–		59	n=3		
Humph	88	n=2	–			
Bray	–		106	n=2		
Locomotion						
Crawl	0	n=7	0	n=6		
Run	31.1	n=7	27.3	n=3	t=1.59	NS
High-sit	53	n=6	43.3	n=3	t=5.08	S
Grooming						
Scratch	–		15.5	n=2		
Fleaing	–		23.5	n=2		
Lick	–		36	n=1		
Alarm	18	n=2	27	n=3	t=−0.77	NS
Feeding						
Wean	32.4	n=7	30.6	n=3	t=0.56	NS
Throw	62.5	n=6	98	n=4	t=−3.2	S
Prey kill (rodent)	121.8	n=5	140	n=2	t=−1.3	NS
(crab)			129	n=1		
Marking						
Urination	–		27.5	n=2	SD=0;	no t-test
Defaecation	31.8	n=7	35	n=2		
Anal marking	46.5	n=7	–			
Cheek marking	60	n=1	–			
Play						
Biting	29	n=5	29	n=3	t=0	NS
Dyadic	32.4	n=5	33.5	n=2	t=−0.29	NS
Object	26	n=2	38	n=1		
Mounting	–		202.5	n=2		
Copulation	295	n=5	256	n=1		
Sibling fighting	256	n=2	301	n=3	SD=0;	no t-test

In hand-raised mongooses grooming developed early, but scratching was inefficient during the first few days. By day 29 scratching was well co-ordinated. The fleaing response (Ewer 1963) resulted from rubbing the mongooses on either the tail base or the shoulder/neck area. Grooming was deemed effective from day 36 when the mongooses began tending to their pelage more carefully. Data regarding the development of grooming in naturally reared animals are lacking due to their confinement in the nestbox during the first few weeks.

The fear response involved several behavioural components, including mouth opening, a harsh abrupt expiration, and freezing (tonic immobility). One or more of these patterns occurred when the young were suddenly disturbed. The onset of the alarm response coincident with eye opening indicated that the stimulus was visual.

The beginning of weaning varied from day 29 to day 40 in naturally raised mongooses, and was not significantly different from the onset in hand-raised animals (Tab. 2). It was followed by a rapid increase in solid food intake. Suckling did not stop at the commencement of weaning, but was phased out over a long period, with some young still sucking the mother's teats until day 108. The sucking response was particularly well-developed, as shown by a pair of hand-raised mongooses (EA and EB) that sucked on each other's genitalia in the absence of the mother's teats. This continued well beyound weaning, and was still observed when the pair (a male and a female) were ten months old.

When presented with live small mammal prey at 67 days of age (white mice) naturally raised young (AA, AB, AC) seemed unaware of the method of prey capture. The mother initially caught and killed the prey within view of her offspring, and then encouraged them to take it from her by shaking her head and drawing attention to the food. She relinquished the prey as soon as the young showed interest, and even appeared to encourage food envy by pulling away if interest in it waned. When live prey were introduced 30 days later, the mother held back and allowed the young to investigate it, and also attempt killing. Killing was not immediately achieved, and the young were more interested in playing with the injured animal. After approximately 20 min the mother dispatched the prey, and by virtue of her interference promoted food envy and consumption. Prey capture and killing was only achieved on day 135 in these mongooses. While naturally raised EC and ED captured their first prey at 102 days, killing was achieved incidentally over a long time by shaking and injuring the mice. Hand-raised mongooses (EA and EB) were given live prey at 140 days. The mice were bitten in the head region and killed in approximately 30 seconds, and then played with prior to consumption. Both hand-raised and naturally reared young began to eat from the anterior end. First encounters with *Xenopus* were different in that both naturally reared and hand-raised young encountered frogs in the ponds between 80 and 89 days, and immediately began to search for them by feeling over the pond substrate. When the frog was captured, possession was maintained by 'hip-slamming' and growling. Although a killing bite was not administered, the young dealt with the prey in adult fashion (BAKER 1989).

The throwing response relates to the method used by some mongooses in immobilising crabs, as well as in egg-breaking. Throwing matured over approximately one month. It began with holding and fiddling with an object between the forefeet, with the mongoose lying either on its side or on its ventral surface; it progressed to lifting the object in the bipedal stance; then to dropping it often accidentally; and finally the intention of downward throwing developed. The discovery of the food content of the eggs was revealed by accidental egg-breaking in hand-raised mongooses, and by the mother breaking them open for her young in natural circumstances.

Discussion

Mortality in marsh mongoose litters has been recorded at Berlin Zoo by FRESE (1980). Factors contributing to the deaths were suggested to be the presence of a conspecific of the same sex or lack of experience of the mother. While the effect of the presence of a male during parturition and the subsequent early development of the young was a cause for concern, it appeared that from eight weeks onwards the young and their mother suffered no ill-effects from the re-introduction of the male. The present study confirmed the adverse effects of the presence of more than one conspecific other than the mother (i.e. a male and a female) on the survival of a litter during parturition. On the other hand the presence of a single male during parturition and the following few days appeared to have no ill-effects. The male clearly did not participate in rearing the young, however, and it is unlikely that a male marsh mongoose which was actively avoided in the natural environment would remain in the vicinity of a mate with young. Exclusively maternal care seems more likely. The solitary nature of marsh mongooses, and the general lack of co-operative behaviour patterns, suggest that females habitually rear young in the absence of a partner. This contrasts strongly with the "helper" system which predomination in the more social mongooses (dwarf mongooses – Rasa 1989; suricates – Ewer 1963; banded mongooses – Rood 1974).

In the nocturnal marsh mongoose the adaptiveness of parturition at night is clear, in that it would allow the mother to remain with her young for the daylight period following birth and perhaps longer, as the nourishment provided by the placental material is adequate to her needs for the first day. Further, the presence of the mother provides both security and nourishment for the young, so that when she does leave to forage the following evening the young are nutritionally satisfied and quiet. Hand-raised young which are not hungry remained asleep and quiet when new-born. When hungry, however, they vocalised loudly which would indicate their presence and attract would-be predators in the natural environment. Even in captivity the mother never abandoned her young for long periods during the first few weeks, and if she was away from the nestbox and heard the young vocalising she returned immediately, which effectively silenced them.

The scruff-hold method of transporting offspring is widespread amongst mongooses and results in the young curling up into the 'Tragstarre' posture (Zannier 1965). The effect of a scruff-hold was two-fold: firstly, it promoted a curling response which prevented the young from bumping over the ground, given the short forelimb length of the adult mongoose; secondly, it appeared to render the young helpless and inhibited struggling, which was essential for efficient transportation. Rasa (1985) showed that disturbed dwarf mongooses moved their young to a new and safer nest. It is likely that *Atilax* would act similarly, as illustrated by the mother transporting her young about the enclosure whenever disturbed.

Details of vocalizations are provided in Baker (1988). The attention call was exclusively a juvenile sound and showed structural affinity with the 'humph' call of adults. The main difference appeared to be in the marked frequency modulation of the attention call (Baker 1988). The last use of the attention call coincided with increased locomotory capabilities in hand-raised mongooses and probably signalled the ability of the young to remain near the mother by their own efforts. As this also coincided with weaning it is likely that the young begin to accompany the mother on short foraging trips at this age. Field data are required to substantiate this in naturally raised mongooses.

Weaning coincided closely with the eruption of the canines on day 29 and premolars on day 33 (Baker and Meester 1986). Continuation of suckling beyond the age of nutritional dependency on the mother may have helped to ensure that the bond formed between mother and young remained intact until the young were fully capable of survival on their own.

It was clear that young marsh mongooses had to learn how to deal with terrestrial prey, both through maternal guidance and experience. However, as soon as it was established that small moving objects were potential prey, mongooses were able to adapt their killing behaviour accordingly. Food envy appeared to play a role in encouraging the young to eat solids, and a maternal feeding growl stimulated attempts to retrieve prey from maternal possession. 'Hip-slamming' has been described by Rasa (1973a) in dwarf mongooses. In *Atilax* it developed around day 34, soon after the start of solid food intake, and appeared to contribute to the complex of behaviour patterns associated with food envy.

The fact that there is no significant difference in the onset of prey killing between naturally raised mongooses and hand-raised ones is not surprising as prey killing is an ability which develops with maturation of skills, such as speed of movement as well as ability to deliver a killing bite. In mongooses prey killing is most often a result of a bite directed at the crown of the head, such that the canine teeth inflict a fatal wound (Baker 1989; Rasa 1973a). Only when mongooses have reached a certain level of development will the killing bite be successfully administered. For this reason, perhaps, the attempt by naturally raised mongooses to kill prey at 102 days was unsuccessful. In the case of the crab kill by a hand-raised animal (K) at 129 days, the method of killing is different from that of rodent capture. Marsh mongooses usually dispatch this prey by throwing it onto the ground (Baker 1989).

In capturing aquatic prey the necessary techniques of 'feeling' and searching for submerged food appeared to be ones which required no learning in both naturally and hand-raised mongooses. From an early age the mongooses manipulated objects between the forefeet on the ground, almost as if unconsciously. The heightened sensory capacity of the feet and the associated elaboration of the neocortex in the brain (Radinsky 1975) may account for the immediate competence of forefoot activity.

In general results show little difference in the rate of development of behaviour patterns in naturally-raised and hand-reared mongooses. However, pattern of development was different where maternal guidance was involved, such as in the development of prey killing patterns.

Detailed work on the postnatal behavioural development of herpestines is scarce. Table 3 summarises available information and shows close similarities in feeding patterns, locomotory development, grooming patterns and alarm responses amongst the six genera.

Table 3. **Postnatal behaviour development in herpestines**
Ages given in days

Character	*Mungos*	*H. ichneum.*	*Suricata*	*Helogale*	*Galerella*	*Atilax*
High-sit	16	60	23–33			42–53
Wean	19	32–64	30–63	35–40	49–63	29–40
Alarm	12		12		14–25	11–35
Fleaing				11–25	18	23–24
Egg break (hen)				75	203	52–130
Rodent kill			78	66	63	102–140
Play-biting	21			30		17–35
Anal drag	23			29–44		35–55
Cheek mark	40			24–39		60
Run well		28	21–40	24		26–35
Defaecate alone			22			29–39
Scratch			2			2
Lick well			30			36
Purring alone	present		present	present	present	absent ?grizzle

Sources: *Mungos* – Rood (1975), Viljoen (1980); *Herpestes ichneumon* – Rensch and Dücker (1959), Dücker (1965), Ben-Yaacov and Yom-Tov (1983); *Suricata* – Dücker (1962, 1965), Ewer (1963); *Helogale* – Dücker (1965), Rasa (1973a, b, 1977, 1985), Rood (1983); *Galerella* – Jacobsen (1982); *Atilax* – Baker (1987), present study.

Resemblance in the rate of postnatal physical development (Baker and Meester 1986) is probably the underlying cause of this similarity, as development of certain behaviour patterns is clearly contingent upon development of locomotor abilities and visual ability, for example. The development of the alarm response is the clearest example of this, as vision is the faculty which releases this behaviour pattern. In *Atilax* eye-opening occurs around day 11 (Baker and Meester 1986) and the alarm response develops on the same day. Eye-opening in *Mungos* begins on day 8 with alarm reactions developing on day 12 (Viljoen 1980), while in *Suricata* eyes open around day 12 and the alarm response is shown on the same day (Ewer 1963).

The development of the 'high-sit' (Ewer 1963) or 'Männchenmachen' (Dücker 1962) showed some variation in maturation with social species developing the pattern earlier (Tab. 3). It seems likely that in the natural environment it would be more adaptive for the sociable species, such as *Mungos* and *Suricata*, which are also diurnal and which rely on